L.M.B.C. MEMOIRS

III.

ECHINUS

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Liverpool Marine Biology Committee.

L.M.B.C. MEMOIRS

ON TYPICAL BRITISH MARINE PLANTS & ANIMALS

EDITED BY W. A. HERDMAN, D.Sc., F.R.S.

III.

ECHINUS

BY

HERBERT CLIFTON CHADWICK

Curator of the Port Erin Biological Station

(With 5 Plates)

PRICE EIGHTEENPENCE

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EDITOR'S PREFACE.

THE Liverpool Marine Biology Committee was constituted in 1886, with the object of investigating the Fauna and Flora of the Irish Sea.

The dredging, trawling, and other collecting expeditions organised by the Committee have been carried on intermittently since that time, and a considerable amount of material, both published and unpublished, has been accumulated. Thirteen Annual Reports of the Committee and four volumes dealing with the "Fauna and Flora" have been issued. At an early stage of the investigations it became evident that a Biological Station or Laboratory on the sea-shore nearer the usual collecting grounds than Liverpool would be a material assistance in the work. Consequently the Committee, in 1887, established the Puffin Island Biological Station on the North Coast of Anglesey, and later on, in 1892, moved to the more commodious and convenient Station at Port Erin in the centre of the rich collecting grounds of the south end of the Isle of Man.

In these twelve years experience of a Biological Station (five years at Puffin Island and seven at Port Erin), where College students and young amateurs formed a large proportion of the workers, the want has been constantly felt of a series of detailed descriptions of the structure of certain common typical animals and plants, chosen as representatives of their groups, and dealt with by specialists. The same want has probably been felt in other similar institutions and in many College laboratories.

The objects of the Committee and of the workers at the Biological Station have hitherto been chiefly faunistic and speciographic. The work must necessarily be so at first when opening up a new district. Some of the workers have published papers on morphological points, or on embryology and observations on life-histories and habits; but the majority of the papers in the volumes on the "Fauna and Flora of Liverpool Bay" have been, as was intended from the first, occupied with the names and characteristics and distribution of the many different kinds of marine plants and animals in our district. And this faunistic work will still go on. It is far from finished, and the Committee hope in the future to add greatly to the records of the Fauna and Flora. But the papers in the present series are quite distinct from these previous publications in name, in treatment, and in purpose. They will be called the "L.M.B.C. Memoirs," each will treat of one type, and they will be issued separately as they are ready, and will be obtainable Memoir by Memoir as they appear, or later bound up in convenient volumes. It is hoped that such a series of special studies, written by those who are thoroughly familiar with the forms of which they treat, will be found of value by students of Biology in laboratories and in Marine Stations, and will be welcomed by many others working privately at Marine Natural History.

It is proposed that the forms selected should, as far as possible, be common L.M.B.C. (Irish Sea) animals and plants of which no adequate account already exists in any text-book. Probably most of the specialists who have taken part in the L.M.B.C. work in the past, will prepare accounts of one or more representatives of their groups. The following have already promised their services, and in some cases the Memoir is already far advanced. The

first Memoir appeared in October and the second in December, 1899, the third is now published, and the fourth will be issued early in March: others will follow, it is hoped, in rapid succession.

Memoir I. ASCIDIA, W. A. Herdman, 60 pp., 5 Pls., 1s. 6d.
II. CARDIUM, J. Johnstone, 92 pp , 7 Pls., 2s.
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ARENICOLA, J. H. Ashworth.
ANTEDON, H. C. Chadwick.
OYSTER, W. A. Herdman and J. T. Jenkins.
PORPOISE, A. M. Paterson.

In addition to these, other Memoirs will be arranged

for, on suitable types, such as *Sagitta*, *Carcinus*, an Amphipod and a Pycnogonid.

As announced in the preface to Ascidia, a donation from Mr. F. H. Gossage of Woolton met the expense of preparing the plates in illustration of the first few Memoirs, and so enabled the Committee to commence the publication of the series sooner than would otherwise have been possible. A second donation recently received from Mr. Gossage is regarded, by the Committee, as a welcome encouragement, and will be a great help in carrying on the work.

W. A. Herdman.

University College, Liverpool,
February, 1900.

L.M.B.C. MEMOIRS.

No. III. ECHINUS.

BY

H. C. CHADWICK.

THE common sea-urchin, *Echinus esculentus*, is the edible Echinoid well-known to marine zoologists as the *Echinus sphæra* of Forbes's "History of British Starfishes." It is found all around the British islands wherever a rocky or stony bottom and an abundant growth of *Fucus* and *Laminaria* provide its favourite haunt. It occurs also in the North Sea and the Mediterranean, off Port Natal, and on the John Adams Bank off the coast of Brazil. Its vertical range is from low-water mark down to 110 fathoms. In the L.M.B.C. district it is common on the Anglesey coast, and especially so off the south end of the Isle of Man. In Port Erin Bay it may be collected by hand on the beach, and on the ruined breakwater at low-water of spring tides; and it is seldom that a haul of the dredge is taken without one or more specimens being included. It does not appear to be used as food in any part of the district.

THE EXTERIOR AND THE TEST.

The test of an adult specimen is more or less pentagonal when viewed from above, the corners being gently rounded. In profile it is usually well rounded, but in some specimens

it is sub-conical, in others depressed. The region immediately surrounding the peristome (Pl. I., fig. 7, *per.*) is somewhat flattened. The outline seen when the test is viewed from either pole is the ambitus. The spines, with which the test is thickly covered, are usually whitish at their bases, more or less of their distal ends being tinged with pale violet. In what appears to be a rare colour variation, the spines are white, with an ill-defined blackish band about the middle of their length. In addition to the spines, the test bears a large number of pedicellariæ (Pl. II.). The mouth (Pl. I., fig. 7, *mo.*) occupies the centre of the broader and slightly flattened pole—hence the oral pole—of the test, and from it may be seen projecting five calcareous teeth (*to.*). It is surrounded by the membranous peristome. The anus (Pl. I., fig. 1, *an.*) is situated at the opposite pole of the test, a little to one side of the centre of a smaller but similarly membranous periproct (*pp.*).

The test is composed of twenty longitudinal rows of calcareous plates (Pl. I., figs. 3 and 4), and ten plates, which encircle the periproct, at the aboral pole. The latter form the so-called apical system (Pl. I., fig. 1). All the plates are firmly united by suture, and growth takes place at their edges, there being a thin and continuous layer of uncalcified connective tissue between the apposed margins. Of the twenty longitudinal rows of plates five double rows form the ambulacra or radii; the remaining five double rows alternate with them, and form the interambulacra or interradii. The structure and relations of the several kinds of plates will be readily understood by reference to figs. 1, 3, and 4, Pl. I. Figure 3 represents two plates taken from one row—the right, facing the observer—of an ambulacrum, in the region of the ambitus. The triangular ends on the left were apposed to exactly

similar plates in the left row of the ambulacrum; those on the right were similarly apposed to one of the plates of the adjacent interambulacrum. It follows from this arrangement that the suture uniting the two rows of plates of an ambulacrum forms a slightly irregular zigzag line. Examination of such an ambulacral plate with a lens reveals two oblique sutures (*sut.*), which sub-divide it into three minor plates. Each of these is traversed by a pair of pores (*po.*), through which the tube feet communicate with their ampullæ (Pl. IV., fig. 29), hence they are called pore plates.

The great majority of the ambulacral plates bear one large tubercle, and a variable number of smaller ones, upon which spines and pedicellariæ are seated. The apical extremity of each ambulacrum is composed of two small pore plates, which usually meet in the middle line. As growth of the test, as a whole, proceeds, such primitive plates are added between those already formed and the radial plates of the apical system; and it is by the ultimate fusion of three such primitive pore plates that the ordinary ambulacral plates are formed. As new pore plates appear, their predecessors are pushed towards the oral ends of the ambulacra; and, as they grow unequally, some remain in contact at the median suture, and are called primary plates. Others are pushed aside from the suture, and are called secondary plates. The outer ends of all the primary and secondary plates, except those last formed at the apices of the ambulacra, are in contact with the plates of the adjacent interambulacra.

The plates of the interambulacra (Pl. I., fig. 4) are similar in shape to those of the ambulacra, but are much larger, and are not sub-divided by suture. Each of the four or five last formed in each row bears one primary tubercle, and a variable number of very small ones. The

number of the former increases with age until, just below the ambitus, there may be from eight to twelve, according to the size of the test. The number of secondary and very small tubercles increases in like manner with the size of the plate. As the peristome is approached some of the tubercles disappear by absorption.

Of the ten plates which form the apical system of the test, five larger ones (Pl. I., fig. 1, *bas.*) immediately surround the periproct, and are usually in contact with each other by portions of their lateral edges. These coincide in position with the interambulacra, and are called basals or genitals, from the fact that each one is perforated near its apex by a pore (*gp.*) through which the spermatozoa or ova escape from the corresponding gonads. Each basal plate usually bears three primary tubercles, and a variable number of smaller ones; and one, the right anterior (*mad.*), is traversed by a large number of fine tubules through which the madreporic tube or sand canal of the water-vascular system is placed in communication with the exterior (Pl. III., fig. 24). This plate is the madreporite. The remaining five plates (*rad.*) are the radials. They are partially wedged in between the basals, and coincide in position with the ambulacra. In some few cases they completely separate the basals and form part of the boundary of the periproct. Each one bears a variable number of small tubercles, and is perforated by a small pore through which the terminal tentacle of the water-vascular canal is protruded (Pl. I., fig. 1). The terminal tentacles are pigmented, and were formerly supposed to be eyes; hence the term oculars, by which the radial plates are commonly known. The periproct is covered by irregular plates, the number of which increases with the age of the test. It has been shown that these occupy the position of an originally single plate, the dorso-central.

If an Echinus be placed mouth downwards, with the interambulacrum in which the madreporite is placed forming the right anterior (Pl. I., fig. 1), it will be found that one ambulacrum is anterior and one interambulacrum posterior. The anterior ambulacrum, with its fellows on the right and left, form the trivium; the remaining two, bounding the posterior ambulacrum, constitute the bivium. According to Lovèn's formula, the ambulacra forming the trivium are numbered, counting from right to left, I., II., and III.; the left bivial ambulacrum is IV. and the right one V.

The membranous peristome has embedded in it a number of detached plates, of which ten, much larger than the rest, are arranged in pairs, coincident in position with the ambulacra, and close to the margin of the mouth. These are the buccal plates (Pl. I., fig. 2). Each one is traversed by a double pore, and bears a corresponding tube-foot of relatively large size (Pl. I., fig. 7, *t.f'.*), in addition to minute clavate spines and pedicellariæ (fig. 7). The peristomial edge of the test bears five arches, which project upwards into its interior, and are connected by intermediate ridges. Each arch (Pl. III., fig. 23; Pl. V., fig. 37, *au.*) is an auricula, and is formed by a process or apophysis from each of the marginal plates of an ambulacrum, which bend towards each other and unite in the middle line, the point of union coinciding exactly with the median suture of the ambulacrum. The intermediate ridges are formed by apophyses arising from the marginal plates of the interambulacra, which unite with each other and with the auriculæ to form the perignathic girdle.

The external surface of the body is covered by an ectoderm, which is everywhere ciliated except upon the sucker discs of the tube-feet. The filamentous ends of many of the cells become continuous with the fibres of a nerve plexus

which lies beneath. Within this is a connective tissue layer of considerable relative thickness, in which the skeletal structures are developed. The calcareous substance of the test and spines takes the form of a more or less dense network, the meshes of which are everywhere filled with a protoplasmic ground substance. The ciliated epithelium of the body cavity may be in direct contact with the last-named, or a layer of muscular fibres may appear between the two.

The spines taper gradually from their bases to their more or less blunt tips, and are elegantly grooved from end to end. The base of each spine presents a saucer-shaped socket to the rounded tubercle of the test (Pl. I., figs. 1, 3, and 4) with which it is movably articulated. A capsular ligament binds the two together, and the movements of the spine are effected by the fibres of a similar capsular muscle, which lies outside the ligament. When viewed in transverse section the calcareous meshwork of the spines presents an elaborate pattern. A transverse section of a decalcified spine (Pl. II., fig. 20) shows that the fusiform cells of the ectoderm are arranged in linear groups, coincident in position with the ridges which traverse the spine from base to tip. Their basal ends are continuous with processes of the cells which form the ground substance of the spine. Though the spines are mainly protective, they also assist locomotion. A healthy Echinus placed on a hard surface, out of water, at once begins to move, solely by the aid of the primary spines of the oral face of the test.

Large numbers of pedicellariæ are scattered over the surface of the test and peristome. They are modified spines, and are attached to the test by ball and socket joints. There are four well-marked forms, but all agree in

the possession of a long stalk and a head composed of three blades.

The largest form is the tridactyle (Pl. II., fig. 13). A calcareous rod gives rigidity to about two-thirds of the length of the stalk, the remainder of which is flexible, and capable of movement in every direction. The blades composing the head are long and slender, and meet only at their bases and apices when apposed to each other. Ligamentous fibres bind the blades together; and they are moved upon each other by three powerful adductor muscles (Pl. II., figs. 13, 16, 19, and 21, *ad.m.*) which run between their adjacent sides. Nerve fibres pass upwards in bundles from the stalk, and are distributed to the sensory cells of the epithelium which clothes the inner surface of each blade (Pl. II., fig. 16, *nf.*).

The second form is the ophiocephalous or snake headed (Pl. II., fig. 15). In it the calcareous rod which supports the stalk is relatively shorter than that of the tridactyle form. The three blades forming the head are scoop-like, with blunt apices, and each one has a sort of handle at its base. Figure 19 represents the head, with blades open, of a very similar but much smaller form which occurs in numbers on the peristome.

The third form is the trifoliate, in which the blades of the head are broad and leaf-like, and meet only along their lateral edges when closed (Pl. II., fig. 17). The ectoderm forms a thick cushion on the inner face of each.

The fourth form is the gemmiform or glandular (Pl. II., fig. 14). In it the calcareous rod of the stalk extends to the head, which is consequently much less capable of independent movement. The apex of the calcareous skeleton of each blade is directed inwards and forms a strong tooth, to which are added several smaller teeth. Each blade contains a glandular sac (Pl. II., figs. 21

and 22, *gl.s.*), which lies outside the skeletal piece, and is bifid at its distal end in many cases. This sac has a glandular epithelium (*gl.ep.*), and is invested by a layer of circularly disposed muscular fibres (*mg.*). Near the apex of the sac is a minute aperture (*ap.*). On the inner face of each blade, just above the level of the adductor muscles, the ectoderm forms a projecting cushion (*tc.*). The cells forming this stain deeply, and, in addition to cilia, are said to bear tactile hairs. A nerve (*nf.*) passes upwards along the inner face of each blade, and its fibres become continuous with the filiform basal ends of the cells forming the cushion.

The function of the pedicellariæ has been the subject of much speculation and experiment. Romanes* concluded from his experiments that they assist locomotion by seizing foreign objects and holding on until the tube-feet can be brought into play, but he does not discriminate between the different forms. Other observers have regarded them as organs adapted to the capture and conveyance to the mouth of small animals, such as worms, Crustacea, &c., to be used as food. Others again have held that they are employed in freeing the neighbourhood of the anus from fæces, and the spines and test from injurious foreign particles. Prouho† found that the glandular pedicellariæ of *Strongylocentrotus lividus* were used to repel the attacks of hungry starfishes. It has been noticed that when a soft bodied animal, such as *Aplysia punctata*, comes in contact with an Echinus it always carries away with it a number of the glandular pedicellariæ.

In addition to spines and pedicellariæ, the plates of the ambulacra bear a number of minute knob-like organs, which project freely from the surface of the test. These

* "Jelly-fish, Starfish, and Sea-urchins," Int. Sci. Ser., vol. L., p. 253.

† Comptes Rendus, CXI. (1890), pp. 62—4.

are the sphæridia (Pl. II., fig. 18). They consist essentially of a hard, calcareous sphere, which differs from the ordinary skeletal structures in being concentrically laminated (*sph.*) The typical sphæridium is described as resting upon a short calcareous stalk, but this does not appear to exist in the present species, its place being taken by a cushion of nerve fibres. The typical sphæridium has also a circular nerve ganglion and a capsular muscle around its base, the ectoderm covering which is specially thickened and bears long cilia. The sphæridia are most probably sensory organs, and have been variously supposed to have an auditory or gustatory function, or, perhaps, to be concerned in the orientation of the test.

At the peripheral edge of the peristome five pairs of hollow, branched appendages project freely outwards, and form the external gills (Pl. I., fig. 7, *ex.g.*). One pair lies in each interradius, and the peristomial edge of the test is slightly notched for their reception. Their contractile walls consist of the ectoderm, of which the cells are deep and bear long cilia; a connective tissue layer containing C-shaped spicules and cribriform plates (Pl. I., figs. 5 and 6), and an inner epithelium continuous with that which lines the body cavity. The cavities of the gills open into the peri-œsophageal sinus.

Alimentary Canal and "Aristotle's Lantern."

The mouth is situated in the centre of the peristome, and the five pointed teeth project from its rounded opening. It opens directly into the pharynx (Pl. I., fig. 12, *ph.*), which passes upwards through the centre of the masticatory apparatus, or "Aristotle's lantern." The latter consists of twenty principal skeletal pieces, which together form a pyramid with five rounded sides, and a complex system of muscles and ligaments (Pl. III., fig. 23; Pl. V., fig. 37).

The great bulk of the pyramid consists of five pairs of jaws, each pair forming an alveolus (Pl. I., figs. 9, 10, and 12, *alv.*). Each alveolus is a hollow, triangular pyramid (fig. 11), two of the surfaces of which are lateral (figs. 9, 11, and 12), and applied to the corresponding surfaces of the alveoli on either side, while the third is outer and slightly rounded (fig. 10). The suture, which marks the line of union of the pair of jaws, runs down the centre of the outer surface (*sut.*). The lateral surfaces are traversed by fine transverse and slightly sinuous grooves (figs. 9 and 12), and the inner edges of these surfaces, which approach each other closely only at the base of the alveolus, are finely toothed. Each alveolus lodges a long, slender, and slightly curved tooth (figs. 9, 10, and 12, *to.*), the hard, pointed tip of which projects beyond its apex. The shaft of the tooth is convex towards, and closely applied to, the inner surface of the rounded outer side of the alveolus (fig. 11), exactly in line with the median suture. Its upper basal end projects some distance beyond the base of the alveolus, and curves upon itself in the direction of the axis of the lantern. A prominent longitudinal ridge or carina traverses the inner concave surface of the tooth from near its pointed tip to a point corresponding with the base of the alveolus. Here the substance of the tooth becomes soft and readily yields to the pressure of the fingers in the form of asbestos-like fibres. Here, too, growth of the tooth takes place. Five oblong intermediate plates, the rotulæ (Pl. I., figs. 8 and 12, *rot.*), rest upon the bases of the alveoli, in such a way as to touch the apposed lateral surfaces of every two, while five slender, curved rods, the radii (Pl. I., fig. 12; Pl. III., fig. 23, *rad.*), lie, one upon each of them. The peripheral ends of the radii are bifurcate, and project over the edge of the pyramid formed by the five alveoli. The alveoli are inter-

radial in position, the rotulæ and radii corresponding with the ambulacra.

Four sets of muscles and one set of ligaments (Pl. III., fig. 23) control the movements of the masticatory apparatus. The adductor muscles of the teeth are broad bands arranged as five pairs (Pl. III., fig. 23; Pl. V., fig. 37, *ad.m.t.*). The two muscles of a pair are attached below to the interambulacral apophyses of the perignathic girdle. Passing upwards they diverge slightly, and are inserted, above, along the outer edge of the arch-like base (Pl. I., fig. 10) of the corresponding alveolus. The contraction of these muscles draws the bases of the alveoli outwards and downwards, while their apices, with their teeth, move inwards towards the centre of the mouth, through which they tend to project. The opening muscles of the teeth (*op.m.t.*) also form five pairs, which run inwards and slightly downwards from the inner faces of the auriculæ to the halves of the alveoli nearest to them. When they contract the teeth are drawn apart, in the direction of the auriculæ, and the mouth is widely opened. The intermediate alveolar muscles run between the apposed lateral faces of the alveoli. Their contraction draws the latter close together, and probably assists in the reduction of the food in the pharynx. The muscles of the radii (*m.r.*), of which there are five, form a pentagonal ring which connects the five radii together; and, by their contraction, probably depress the whole apparatus in the direction of the mouth. A pair of ligaments (*lig.*) are attached to the forked peripheral end of each radius, and, diverging as they pass downwards, are attached to the interambulacral apophysis of the perignathic girdle on either side. The peritoneal membrane which lines the body cavity is continued over the lantern, and forms five projecting sacs, in which the soft bases of the alveolar

teeth lie. The included space forms part of the cœlom, and is the peripharyngeal sinus. It is, however, completely shut off from the general cœlomic cavity.

The pharynx is five-rayed (Pl. IV., fig. 31), and each ray is attached by a pair of bands of connective tissue to the inner edges of the lateral faces of the adjacent alveolus. The pharynx passes into the œsophagus (Pl. III., fig. 23; Pl. V., fig. 37, *œ.*), which ascends from the lantern to the apex of the test. Turning downwards again, the œsophagus passes into the first or inferior spiral of the intestine (Pl. V., fig. 37, *inf.s.*), the commencement of which is marked by a sac-like swelling, and a considerable increase in the diameter of the gut. The inferior spiral makes a complete circuit of the test, running in gracefully undulating folds through radius III. to IV., V., I., and II. into interradius 2. Here the intestine turns upon itself to form the superior spiral (*sup.s.*), which runs through radius II. to I., V., and IV. Thence, but with slightly reduced diameter, it turns again towards the apex of the test to form the rectum (Pl. III., fig. 23; Pl. V., fig. 37, *rec.*), which runs obliquely across interradius 3 to the anus, the opening of which is very small when compared with the diameter of the rectum. Mesenteric strands attach both spirals to the inner surface of the test, and separate from the cœlomic cavity a small space which surrounds the anal end of the rectum, and forms the perianal sinus. Near the point where the œsophagus passes into the inferior spiral, an accessory or co-lateral intestine, the siphon (Pl. V., fig. 37, *si.*), branches off from the intestine, along the inner (axial) side of which it runs to re-enter the main tube at or near the end of the spiral. Both coils of the intestine are extensively sacculated.

In a transverse section of the œsophagus (Pl. IV., fig. 32)

the following layers may be distinguished:—(1) an epithelium (*ep.*) composed of long fusiform cells; (2) a layer of connective tissue (*c.t.l.*) containing, in the inferior spiral, an extensive system of blood lacunæ; (3) a thin layer of muscular fibres (*m.f.l.*); (4) an outer and very delicate layer of connective tissue; (5) the ciliated epithelium of the cœlom (*e.b.c.*). A delicate cuticle (*cu.*) invests the epithelium of the gut, which is also ciliated. In the œsophagus and, to a much larger extent, in the inferior spiral, the epithelium contains numbers of gland cells (fig. 34, *gl.c.*). The relative thickness of the epithelial and connective tissue layers varies in different parts of the intestinal tract. The minute structure of the siphon is the same as that of the intestine. Its function has not been determined, but a suggestion has been made that it may subserve intestinal respiration.

The Echinus is probably wholly carnivorous; and the frequent occurrence, in the intestine, of fragments of the *shells* of barnacles and serpulid worms attests the destructive power of the alveolar teeth.

WATER-VASCULAR SYSTEM.

The water-vascular system consists of tubular canals, which communicate, on the one hand, with the exterior through the pores of the madreporite; and, on the other hand, with the cavities of the tube-feet and their ampullæ. The madreporite (Pl. I., fig. 1; Pl. III., fig. 24, *mad.*) is traversed by a large number of minute pores (*m.p.*), which converge towards and open into a cavity, the madreporic ampulla (*mad.amp.*), which lies beneath it. The external surface of the madreporite is covered by ectoderm cells like those which clothe the general surface of the test; but at the external openings of the pores the character of the cells suddenly changes, and the upper fourth of the

length of each pore is lined by ciliated columnar cells, which stain deeply. Lower down, the columnar cells gradually give place to others of rounded form, which are also ciliated. Some of the pores anastomose with neighbouring ones, but the majority take a nearly straight course from the outer to the inner surface of the madreporite.

The madreporic ampulla communicates through its lower or inner wall with a tubular canal, the madreporic tube or sand-canal (Pl. III., figs. 23 and 24, *w.t.*), lined with ciliated columnar epithelium. This, enclosed within the axial sinus of the cœlom (Pl. III., figs. 23 and 24, *ax.sin.*), runs directly to the base of the lantern, and opens into the circular water vessel (Pl. III., fig. 23, *c.w.v.*), which encircles the œsophagus at that point.

Five roughly pear-shaped and sacculated vesicular bodies, the Polian vesicles (fig. 23, *P.v.*), open interradially into the circular water vessel. From the latter, in each radius, there runs out a radial canal (fig. 23; *Pl.* V., fig. 37, *r.w.v.*) which, passing beneath the rotulæ, down the outer surface of the lantern, and through the arch-like auricula, traverses the whole length of the corresponding ambulacrum, on the inner surface of the test, to its apex, where it ends blindly in the pore of the radial plate (Pl. IV., fig. 30, *r.w.v.*). Before reaching the auriculæ, each radial canal gives off a pair of lateral branches to the corresponding pair of buccal tube-feet (Pl. I., fig. 7; Pl. IV., fig. 33, *t.f′.*) which, unlike the tube-feet to be immediately described, have no ampullæ.

From the auricular archway upwards to their blind extremities the radial canals give off a large number of alternating lateral branches (Pl. III., fig. 23; Pl. IV., fig. 29, *l.b.w.v.*), which open into flattened, thin-walled vesicles, the ampullæ of the tube-feet (Pl. III., fig. 23;

Pl. IV., fig. 29; Pl. V., fig. 37, *am.t.f.*), which project, like the leaves of a book, into the interior of the test. Each ampulla communicates with the cavity of a tube-foot (*l.t.f.*) through two canals (Pl. IV., fig. 29, *c.t.f.*), which traverse a pair of pores of an ambulacral plate. The tube-feet are tubular organs which occur on the plates of the ambulacra only. They are exceedingly mobile, and can be extended far beyond the tips of the spines. Their free, imperforate ends take the form of circular sucker discs, by means of which the animal can attach itself with great firmness to the surface on which it rests.

Examination of a thin section of one of these organs (Pl. III., fig. 27) reveals the following structures:—(1) an external ciliated epithelium (*ect.*) continuous with that of the general surface of the body; (2) a delicate plexus of nerve fibres and ganglion cells; (3) a layer of connective tissue (*c.t.l.*) in which C-shaped calcareous spicules (Pl. I., fig. 5) occur; (4) a layer of longitudinally disposed muscular fibres (*m.f.l.*); (5) a ciliated epithelium lining the cavity of the organ (*ep.*). The terminal sucker is supported by an elegant, ring-like calcareous plate, composed of six or seven segments which, like the C-shaped spicules, lies embedded in the connective tissue layer. The sucker discs of the buccal tube-feet are, in like manner, supported by a ring-like plate, but in conformity with the shape of the discs, they are oval, and composed of four or five segments only. The epithelial cells which cover the external surface of the sucker discs are much longer than those of the tubular portion of the tube-feet, and are not ciliated.

The minute structure of the ampullæ is similar to that of the tube-feet. In a section there may be seen from without inwards:—(1) the ciliated epithelium lining the body cavity; (2) a layer of connective tissue, containing

minute calcareous corpuscles; (3) a layer of circular muscular fibres; (4) an inner ciliated epithelium continuous with that of the radial canal and the cavity of the tube-foot.

The fluid contained in the system of canals, now described, is said to be sea-water, with traces of albumen. It is of a pale yellow or reddish colour; and, in addition to amœboid cells, corpuscles containing pigment are found floating in it. The question of the origin of this fluid has been much debated. The view which meets with general acceptance is, that the cilia borne by the epithelial cells which line the pores of the madreporite and madreporic tube induce a current of sea-water to flow from the exterior through the madreporite; but an exactly opposite view has been maintained. Though locomotion is the primary function of the tube-feet, there can be little doubt that they are also concerned in respiration. An Echinus always retracts its tube-feet when the supply of respiratory oxygen falls short in the water in which it is kept; *but if* the water be changed, the opposite effect immediately occurs, the tube-feet being extended to their fullest capacity, and moved about actively in all directions.

It has been suggested* that the water-vascular system is morphologically and ontogenetically a left nephridium (see account of its development on p. 23), and that the current induced by the cilia of the madreporic pores and water-tube can be shown by experiment to be outwards, and not inwards, as described above. This view has not met with general acceptance and a series of experiments conducted by Ludwig† confirmed the statements of most previous observers with regard to the inward direction of the current.

* Ann. and Mag. Nat. Hist. Vol. XX. (1887), pp. 321—6.

† Zool. Anzeig. XIII. (1890), pp. 377—9.

Nervous System.

The nervous system consists of a ring of nerve fibres and ganglion cells, which encircles the pharynx (Pl. III., fig. 28, *pp.n.r.*) close to the mouth, and five radial trunks (Pl. III., fig. 28; Pl. IV., figs. 29 and 33, *r.n.*) which traverse the entire length of the ambulacra, upon the inner surface of the test, and in close relation with the radial canals of the water-vascular system. From the peripharyngeal ring, in the radii, nerves are given off to the oral integument (Pl. III., fig. 28, *n.ph.*) and the wall of the pharynx, in which they break up to form plexuses.

In traversing the ambulacra the radial trunks give off, at intervals which correspond with the lateral branches of the water-vascular canals, nerves which pass through the ambulacral pores (Pl. IV., fig. 29, *l.n.*), and are distributed to the tube-feet and the periphery of the test. In both cases the fibres become continuous with those of the *sub*-epithelial nerve plexus. In a sagittal section of the distal end of a radial trunk (Pl. IV., fig. 30, *r.n.*) this intercommunication of its fibres with those of the sub-epithelial plexus is specially obvious. In transverse section the peripharyngeal ring and radial trunks present the form of broad bands (figs. 26, 29, and 33). In ultimate structure they consist of ganglion cells, of which a well-marked layer lies upon the peripheral surface, *i.e.*, the surface nearest to the test, and nerve fibres, which run in a longitudinal direction, and amongst which a few ganglion cells are scattered.

In addition to the peripharyngeal nerve-ring and radial trunks, there are five lamellæ, consisting of ganglion cells and nerve fibres, which lie in close proximity to the nerve-ring at the points of origin of the radial trunks. From each lamella a pair of large nerves arise. These ascend

along the edges of the five alveoli, and are supposed to innervate their muscles. This has been described as the "deep oral nervous system," in contra-distinction to the well-known nerve-ring and radial trunks which constitute the superficial oral system.

No specialised sense organs, other than the sphæridia and the terminal tentacles of the water-vascular system appear to have been discovered in *Echinus esculentus*. The tube-feet are highly sensitive to external stimuli, and those of the allied species, *Echinus micro-tuberculatus*, have a tubercle-like thickening of the ectoderm close to the sucker disc, beneath which there is a ganglionic mass of nerve tissue.

Vascular and Cœlomic Systems.

In addition to the radial canal of the water-vascular system, two other canals traverse the ambulacra, in close relation to the radial nerve trunks. One of these is the epineural canal (Pl. III., fig. 28; Pl. IV., figs. 29, 30, and 33, *r.ep.c.*). It runs along the peripheral face of the nerve trunk, between it and the test. At the apex of the latter it ends blindly, in close proximity to the terminal tentacle of the water-vascular canal (Pl. IV., fig. 30, *r.ep.c.*), and, at the opposite extremity, it thins out gradually as the mouth is approached, and does not open into the circular epineural canal (Pl. III., fig. 28, *c.ep.c.*) which surrounds the pharynx. In the Ophiuroidea the epineural canals have been found to arise by the growth of two lateral folds of the integument over the radial nerve trunks. The folds meet and unite and so form the canal-like space. It is probable that further research into the ontogeny of the Echinoidea will prove that their radial canals arise in a similar manner.

The second canal is the pseudhæmal (Pl. III., fig. 28; Pl. IV., figs. 29, 30, and 33, *r.p.h.c.*). This runs along the inner, axial face of the nerve trunk, and, like the epineural canal, ends blindly at the apex of the test. It also does not communicate with the corresponding circular pseudhæmal vessel (Pl. III., fig. 28, *c.p.h.c.*). The pseudhæmal canals contain a fluid similar to that found in the cœlom, and it is possible that their function may be the nourishment of the nerve trunks, with which they are so intimately associated. They give off lateral branches, which run parallel with those of the water-vascular canal and of the radial nerve.

Little is known concerning the ontogenetic history of the pseudhæmal system. The corresponding system in the Holothuroidea has a definite epithelial lining, which points to the conclusion that it is derived from the hydro-enterocœl, and throws doubt upon the schizocœlomic origin which has been claimed for it in the starfishes.

The blood-vascular system of *Echinus* and its allies has been the subject of much discussion, and the descriptions published by Teuscher, Hoffmann, Ludwig, Hamann, Cuénot, Perrier, and Koehler, differ considerably in detail. There are undoubtedly two vessels, which run alongside the inferior coil of the intestine, in the mesentery which supports the latter. One—the ventral vessel (Pl. III., fig. 23, *v.v.*)—runs along the inner axial side of the intestine, and is connected by numerous lacunæ with the dorsal vessel (Pl. V., fig. 37, *d.v.*), which runs on the outer side of the intestine. Both vessels have been described as opening into a circular vessel, which is said to surround the œsophagus in close proximity to, yet quite distinct from, the water-vascular ring-canal. The existence of such a separate circular vessel is, however, open to doubt; and this remark applies with greater force to the blood-vessels

which have been described as radiating from it, and traversing the ambulacra between the water-vascular and pseudhæmal canals. Such vessels are not evident in carefully prepared serial sections of the ambulacra of the present species.

In connection with the blood-vascular system, the central plexus or axial organ may be described. It is a fusiform body (Pl. III., figs. 24 and 25, *cen.pl.*), consisting of a network of connective tissue, which almost completely fills the cavity of the axial sinus (Pl. III., figs. 23, 24, and 25; Pl. V., fig. 37, *ax.sin.*), to the inner wall of which it is attached by connective strands. Its lower, oral end rests upon the circum-œsophageal vascular ring (fig. 23), and is said to open into the blood-vascular ring by those authors who maintain the existence of such a structure. Its upper apical end is attached to and perforates the septum which divides the axial sinus from the madreporic ampulla (Pl. III., fig. 24). The reticulum of connective tissue is densest at the periphery of the organ (Pl. III., fig. 25; Pl. IV., fig. 35). In the deeper cortical portion (fig. 36) the network is much more open, and its fibres more clearly defined. Numbers of nucleated cells of rounded form (fig. 35), from which lymph corpuscles are said to be derived, lie within the meshes of the reticulum. The central plexus has given rise to more discussion than any other structure found in the Echinoderm body; and the names "heart," "kidney," "plastidogenic organ," "lymph gland," indicate the functions which have been ascribed to it by various authors.

In addition to the peripharyngeal or lantern sinus and the axial sinus, the cœlom is further sub-divided by a circular membrane, which connects the anal end of the rectum with the surrounding body-wall, and encloses a small perianal sinus. Below this, another similar mem-

brane encloses a second and slightly larger periproctal sinus.

The fluid which fills the body cavity and sinuses has a peculiar musk-like odour, and is of a pale greyish red colour. It contains a small quantity of albuminoid matter, and has an alkaline reaction. Its specific gravity is the same as that of sea-water. Corpuscles of two kinds are found in it. One of these is a colourless amœboid cell, the finely granular protoplasm of which throws out long filiform and branched pseudopodia. The pseudopodia unite with those of other cells with which they come in contact. This is followed by coalescence of the cell bodies, and the process is repeated until large plasmodia are formed, in which an endosarc and ectosarc become differentiated. The second and rarer kind is a larger cell, also colourless, and containing a number of large, spherical refractive granules. The cœlomic fluid coagulates rapidly when drawn from the test, and a clot is formed consisting of a clear substance, allied to mucine, in which all the corpuscles are included.

Reproductive System.

The reproductive organs or gonads are five arborescent glands, suspended by mesenteric folds from the inner wall of the apical half of the test (Pl. V., fig. 37, *gon.*), and are very similar in position and appearance in the two sexes. They are interradial, and open to the exterior through the pores of the basal plates of the apical system. Before reaching their respective pores, the five genital ducts perforate a ring-like cœlomic sinus which encircles the rectum. This is readily seen in young specimens in which the gonads are not ripe. The walls of the gonads are extensively sacculated, and form numerous follicles, on the inner surface of which the sexual cells are formed.

When sexually mature the male gonads are of a milk-white or creamy hue, while the ovaries are yellowish or orange-brown in colour.

OUTLINE OF LIFE-HISTORY.

During the breeding season the spermatozoa and ova are discharged into the sea, where fertilisation of the ova takes place. Segmentation of the egg is total, though not quite regular, and results in the formation of a spherical blastula (Pl. V., fig. 38), consisting of a single layer of cells, enclosing a large segmentation cavity filled with fluid (*seg. cav.*). Each cell bears a single flagellum on its outer surface, by the vibration of which the blastula revolves.

Following immediately upon the completion of segmentation, a slight depression makes its appearance at one pole (Pl. V., fig. 39), and, at the same time, the cells forming the depression begin to bud actively. The resultant cells (*mes.c.*) are amœboid; and, making their way all over the segmentation cavity or blastocœl, eventually form the muscular and connective tissue systems of the adult. The depression deepens, and forms the archenteron or primitive intestine of the larva (Pl. V., fig. 43, *arch.*). The blastula has now become a gastrula. The dorsal surface of the gastrula is convex; its ventral surface concave; and it is bilaterally symmetrical.

The blastopore (*blas.*) gradually moves forward on to the ventral surface, and the larva enters upon the "Pluteus" stage (fig. 42). At the same time, the first skeletal structures appear in the shape of two lateral calcareous spicules (fig. 42, *sk.r.*), which support the body of the larva and the posterior ventral arms (*p.ven.a.*), which begin, at this stage, to grow out from the ventral surface. The anterior blind end of the archenteric tube now develops, on each side, a small out-growth (fig. 42), which

curves round towards the posterior end of the larva. These are soon separated from the archenteron by a constriction (fig. 40), and then form a single horse-shoe shaped hydro-enterocœlic vesicle (*hy.ent.*). Concurrently with the formation of the vesicle, or immediately following it, the two limbs of the horse-shoe become separated by further constriction, and lie on the sides of the archenteron. The two vesicles again divide into anterior and posterior portions; and the anterior portion of that on the left ultimately opens to the exterior through a water pore, and gives origin to the water-vascular system of the adult. The remaining vesicles are enterocœlic, and ultimately form the lining of the body cavity. After the separation of the hydro-enterocœl vesicle, the blind end of the archenteron bends towards the ventral surface, in which, at the same time, a small invagination of the ectoderm takes place. The two eventually meet, and by the disappearance of their walls at the point of union, become continuous. The ventral invagination becomes the mouth, and the blastopore the anus of the pluteus. Three pairs of arms, in addition to the posterior ventral pair already mentioned, make their appearance and gradually increase in length as growth of the pluteus as a whole proceeds. The body becomes shorter, and its posterior end well rounded (Pl. V., fig. 41).

The metamorphosis of the pluteus into the young Echinoid has not yet been fully described in our species. A flask-shaped invagination of the ectoderm of the left side grows inwards towards the hydrocœl vesicle, to the exterior of which it is applied as the "Echinoid disc." Its floor thickens and becomes discoid, while from the hydrocœl five primary tentacles grow out, pushing before them the Echinoid disc, which is said to form the epithelium, and possibly the radial nerves, of the oral half of the

test of the young Echinus. The apical half of the test is said to be formed directly from the dorsal ectoderm of the pluteus. The four pairs of arms gradually disappear, and their skeletal rods are absorbed.

The young Echinus takes over the larval stomach and the enterocœlic and hydrocœlic vesicles, but the larval mouth and anus are succeeded by corresponding structures formed independently in the young urchin. The water pore, by which the original hydrocœlic vesicle opened to the exterior, becomes the madreporite. Pedicellariæ appear early, even before the close of the pluteus stage. Later on certain of the plates of the test and parts of the masticatory apparatus appear as minute lattice-like plates. Advanced plutei of *Echinus esculentus* have been taken in the tow-net, in Port Erin Bay, early in June, and the young Echini probably take to their adult mode of life towards the end of that month or the beginning of July.

Explanation of the Plates.

Reference Letters.

ad.m.t. adductor muscles.
am.t.f. ampullæ.
an. anus.
ap. aperture of gland.
arch. archenteron.
au. auricula.
ax.sin. axial sinus.
bas. basal plate.
blas. blastopore.
cen.pl. central plexus.
c.ep.c. epineural canal.
c.p.h.c. circ. pseudhæmal canal.
c.t.f. canals of tube feet.
c t.l. connective tissue.
cu. cuticle.
c.w.v. circular water vessel.
d.v. dorsal vessel.
e.b.c. epithelium of body cavity.
ect. ectoderm.
ep. epithelium of intestine.
ex.g. external gills.
gl.c. gland cells.
gl.s. glandular sac.
gon. gonad.
gp. genital pore.
hy.ent. hydro-enterocœl.
inf.s. inferior spiral of intestine.
int.alv.m. inter-alveolar mus.

int.pl. interambulacral plates.
l.b.w.v. lat. branch water vessel.
lig. ligaments.
l.n. lateral nerve.
l.t.f. cavity of tube-foot.
mad. madreporite.
mad.amp. ampulla of ditto.
mes.c. mesenchyme cells.
m.f.l. muscular layer.
m.g. muscular coat of gland.
mo. mouth.
m.p. pores of madreporite.
m.r. muscles of radii.
nf. nerve fibres.
n.ph. nerve to pharynx.
œ. œsophagus.
op.m.t. opening muscles.
per. peristome.
ph. pharynx.
po. ambulacral pores
pp. periproct.
p.pl. peristomial plate.
pp.n.r. peripharyngeal nerve.
P.v. polian vesicles.
p.ven.a. posterior ventral arms.
rad. radii.
rad.pl. radial plates.
rad.ep.c. radial epineural canal.
rec. rectum.
r.n. radial nerve.
r.p.h.c. rad. pseudhæmal canal.
rot. rotulæ.
r.w.v. radial water vessel.
seg.cav. segmentation cavity.
si siphon.
sk.r. skeletal rods.
sph. calcareous sphere of sphæridium.
sup.s. sup. intestinal spiral.
sut. suture.
t. test.
to. teeth.
t.f. tube-foot.
t.f'. buccal tube-feet.
t.t. terminal tentacle.
t.c. tactile cushion.
v.v. ventral vessel.
w.t. madreporic tube.

Plate I.

Fig. 1. The apical system of plates. × 4.
Fig. 2. One of the ten peristomial plates. × 10.
Fig. 3. Two plates from an ambulacrum. × 4.
Fig. 4. A single plate from an interambulacrum. × 4.
Fig. 5. A bihamate spicule from the connective tissue layer of a tube-foot. × 150.
Fig. 6. A cribriform plate from the connective tissue layer of an external gill. × 80.
Fig. 7. The mouth, peristome, and external gills. × 2.

Fig. 8. A rotula. Nat. size.
Fig. 9. An alveolus, viewed from lateral faces. Nat. size.
Fig. 10. An alveolus, viewed from outer surface. Nat. size.
Fig. 11. A transverse section of an alveolus, to show the position of the tooth. Nat. size.
Fig. 12. "Aristotle's lantern," after removal of two of the alveoli to show the pharynx. Nat. size.

PLATE II.

Fig. 13. A tridactyle pedicellaria. × 20.
Fig. 14. A gemmiform or glandular pedicellaria. × 20.
Fig. 15. An ophiocephalous pedicellaria. × 20.
Fig. 16. Longitudinal section of the decalcified head of a small tridactyle pedicellaria. × 175.
Fig. 17. One of the blades of the head of a trifoliate pedicellaria. × 130.
Fig. 18. Vertical section of decalcified sphæridium. × 175.
Fig. 19. Head of a small ophiocephalous pedicellaria from the peristome. × 60.
Fig. 20. A small portion of the periphery of a decalcified spine. × 350.
Fig. 21. Longitudinal section of the decalcified head of a glandular pedicellaria. × 175.
Fig. 22. Transverse section of the decalcified head of a glandular pedicellaria. × 80.

PLATE III.

Fig. 23. Dissection to show the muscles and ligaments of the masticatory apparatus, and the principal canals of the water-vascular system. × 2.
Fig. 24. Part of a sagittal section of the apical system, showing the pores of the madreporite, madreporic ampulla, water-tube, axial sinus, and central plexus. Slightly diagrammatic. × 20.

Fig. 25. Transverse section of axial sinus, central plexus, and water-tube, seen under simple lens. × 8.

Fig. 26. Transverse section of a radial nerve. × 80.

Fig. 27. Longitudinal section of the distal end of a tube-foot. × 180.

Fig. 28. Part of a sagittal section of "Aristotle's lantern" and the adjacent parts. × 55.

Plate IV.

Fig. 29. Diagram of a transverse section of an ambulacrum, showing the relation of the radial canal of the water-vascular system to the tube-feet and their ampullæ. Magnified.

Fig. 30. Sagittal section of distal end of a radial nerve, showing the intercommunication of its fibres with the basal ends of ectoderm cells. × 180.

Fig. 31. Transverse section of the pharynx. × 20.

Fig. 32. Part of transverse section of œsophagus. × 180.

Fig. 33. Part of sagittal section of peristome, showing a lateral branch of a radial canal opening directly into the cavity of a buccal tube-foot. × 55.

Fig. 34. Part of transverse section of inferior coil of intestine, showing numerous gland cells. ×180.

Fig. 35. Part of the periphery of transverse section of central plexus, showing the densely packed nuclei of connective tissue and the rounded cells from which lymph corpuscles are said to be derived. × 400.

Fig. 35. Part of cortex of transverse section of central plexus, showing the loose meshwork of connective tissue. × 400.

Plate V.

Fig. 37. View of the interior of the test of *Echinus esculentus.* The three ambulacra shown are those forming the trivium. One gonad only is shown *in situ.* Nat. size.

Fig. 38. A blastula of *Echinus,* in optical section. × 210.

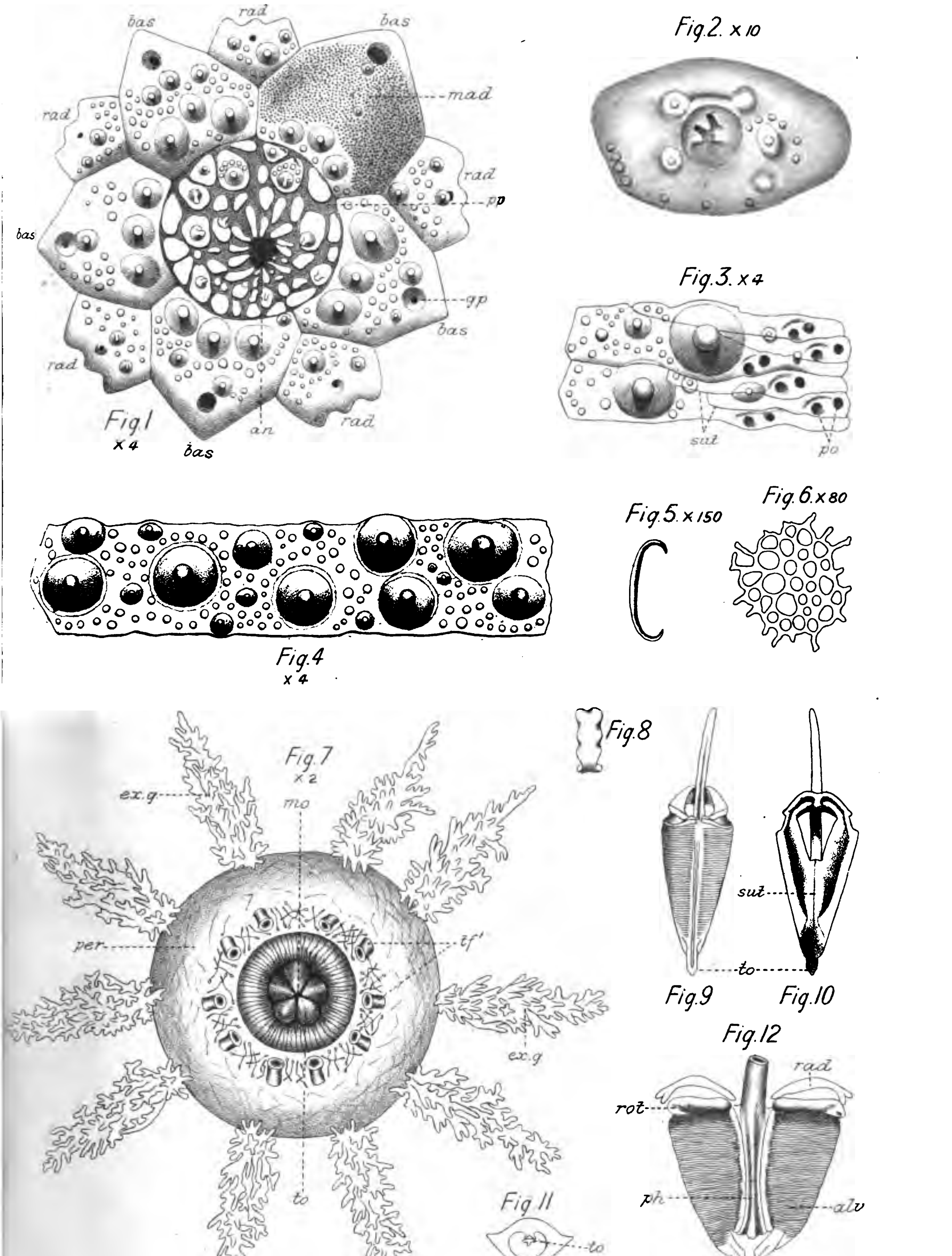
Fig. 39. A blastula passing into the gastrula stage, showing the amœboid mesenchyme cells. × 210.

Fig. 40. Diagram showing the separation of the hydro-enterocœl from the archenteron.

Fig. 41. A fully-developed but not full-grown pluteus of *Echinus.* ×100.

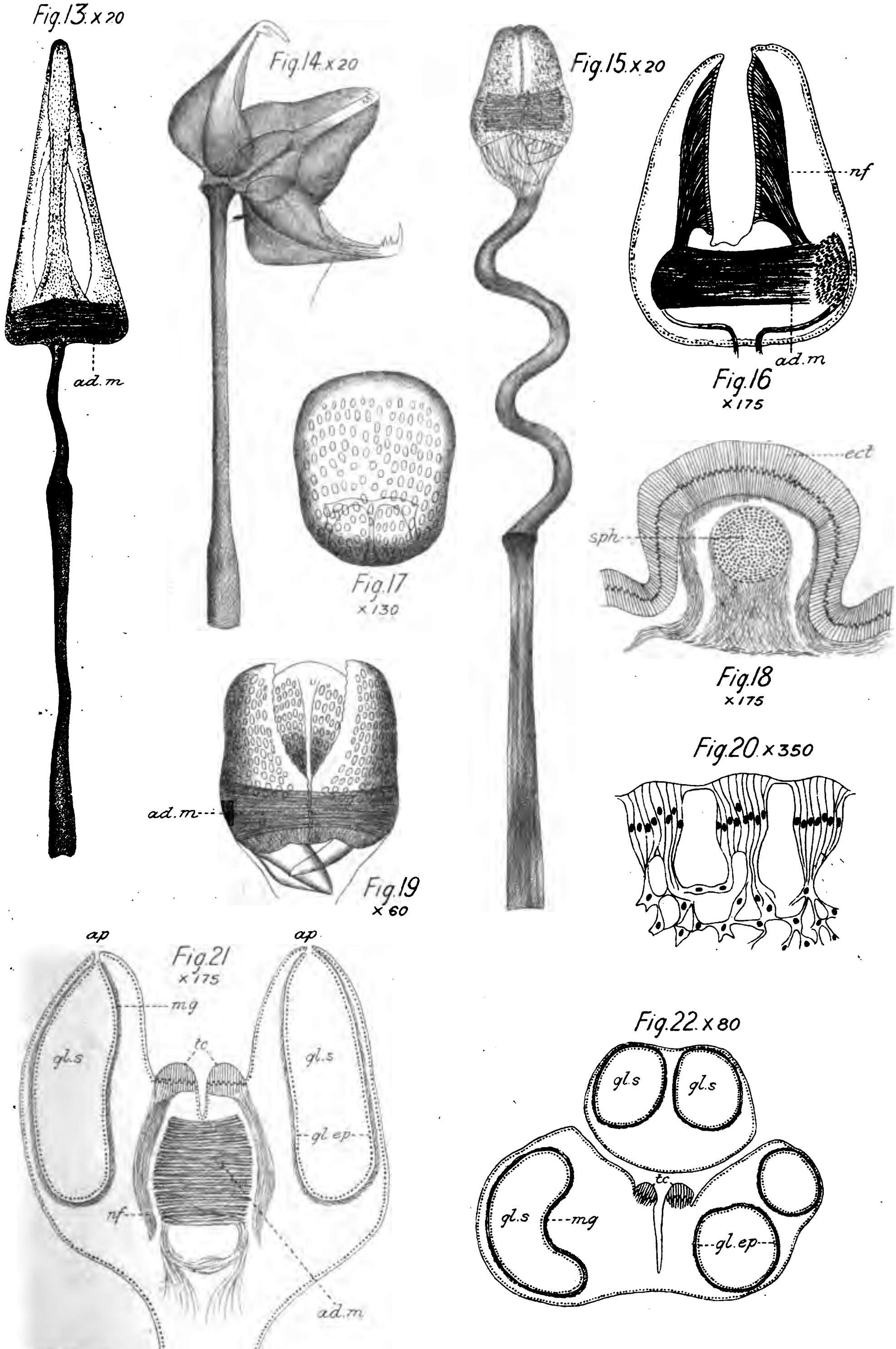
Fig. 42. A pluteus, two days old, showing the beginning of the formation of the hydro-enterocœl. × 170

Fig. 43. A fully-formed gastrula, passing into the pluteus stage. × 210.



H.C.C. del. S.B. lith.

ECHINUS.



H.C.C. del. S.B. lith.

ECHINUS.

Fig. 23. x 2

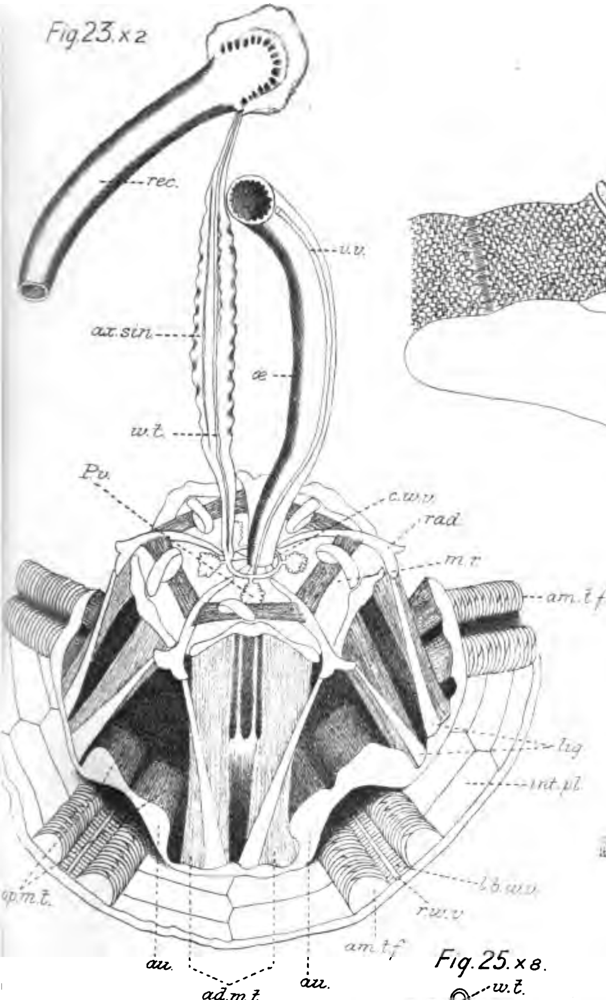


Fig. 24. x 20

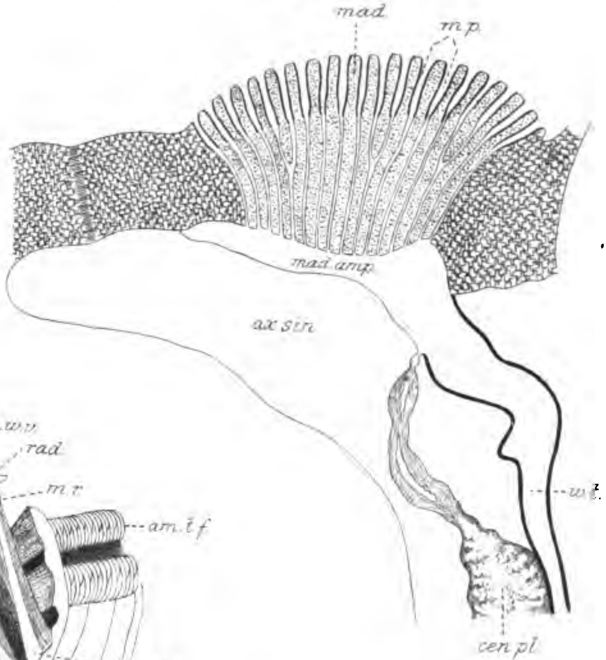


Fig. 26 x 80

Fig. 25. x 8.

Fig. 27 x 180

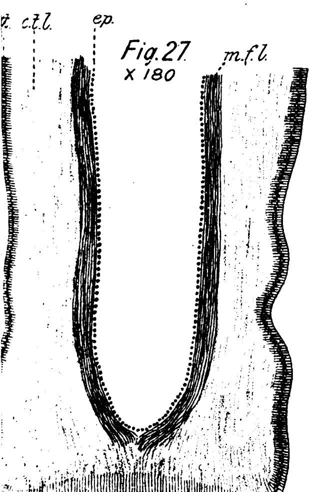
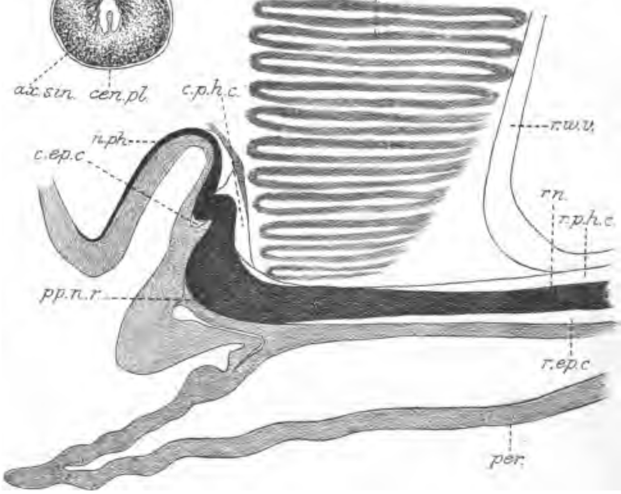


Fig. 28 x 55



C.C. del.

ECHINUS.

S.B. lith.

Fig. 29

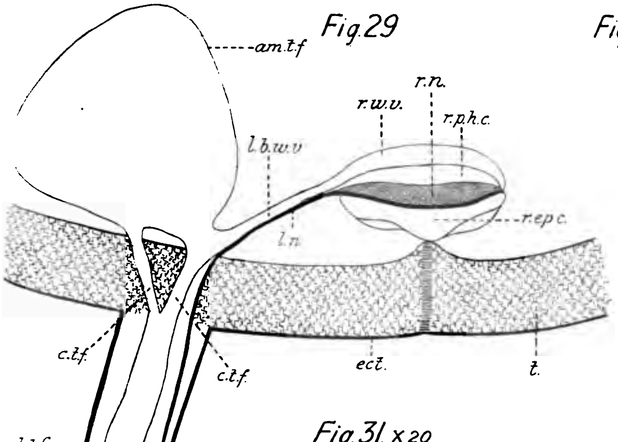


Fig. 30 x 180

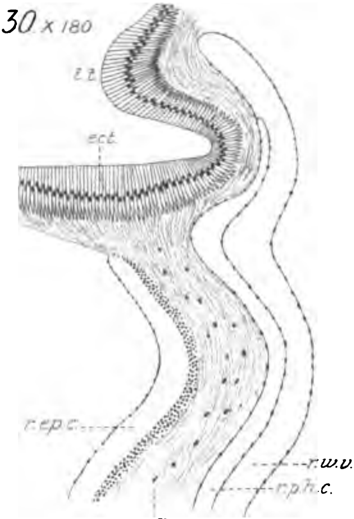


Fig. 31. x 20

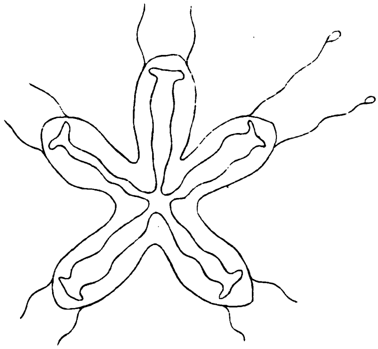


Fig. 32 x 180

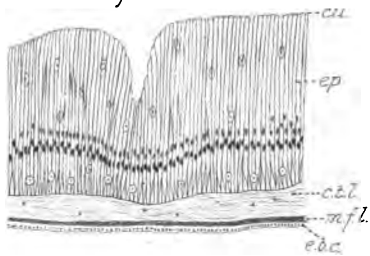


Fig. 33. x 55

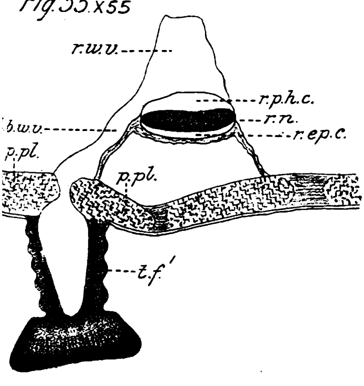


Fig. 34. x 180

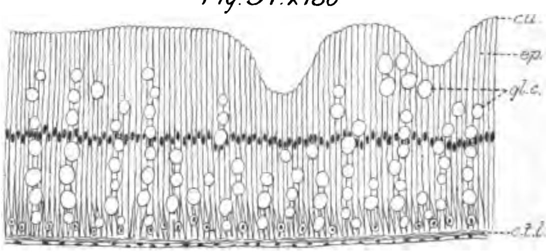


Fig. 35. x 400

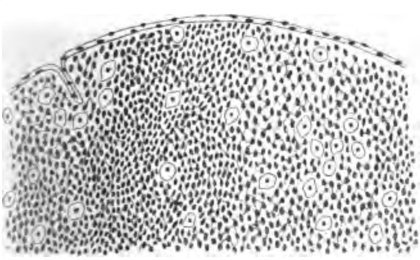


Fig. 36. x 400

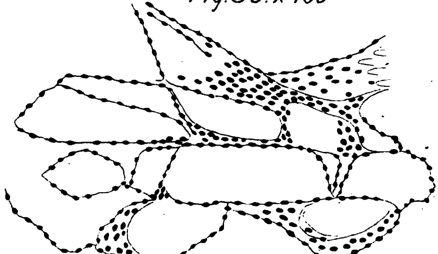


Fig. 37

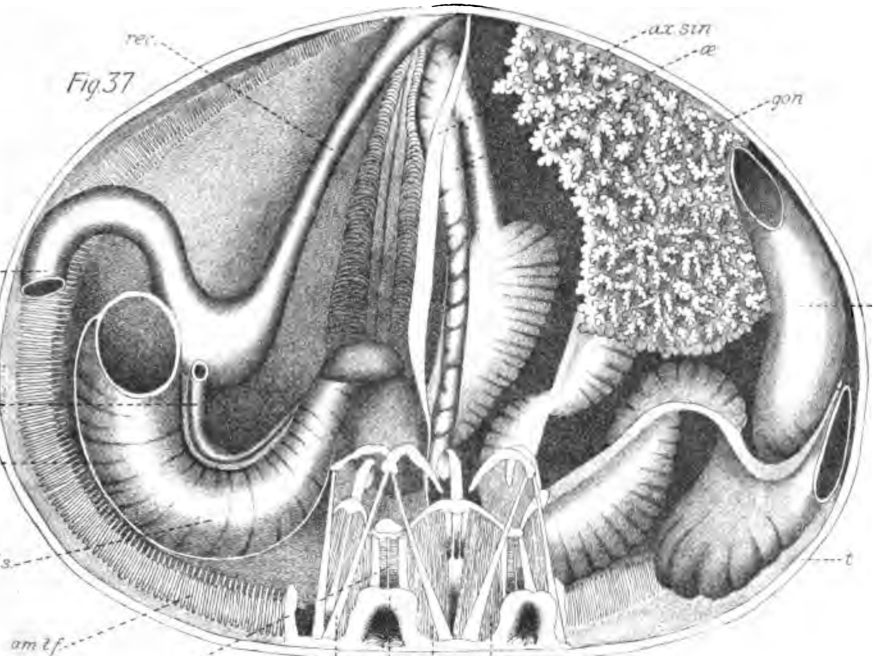


Fig. 38. x 210

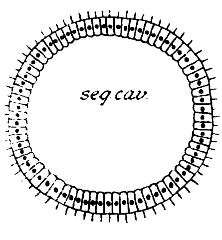


Fig. 40

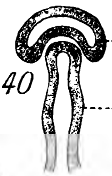


Fig. 41 x 100

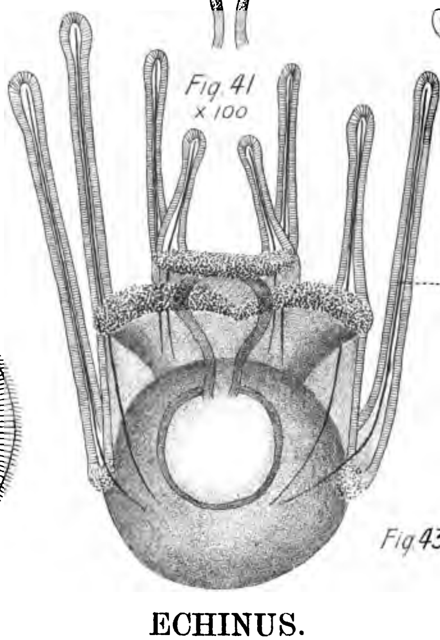


Fig. 42. x 170

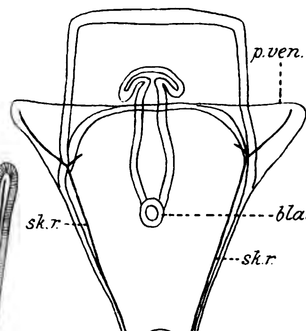
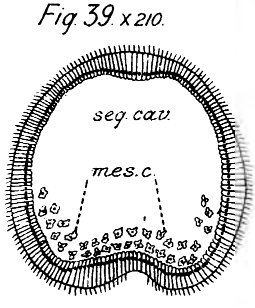


Fig. 39. x 210.



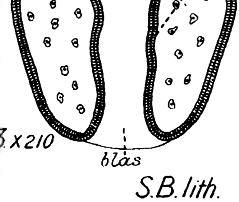


Fig. 43. x 210

H.C.C. del.

S.B. lith.

ECHINUS.